SELECTIVE EPIZOAN ENCRUSTATION OF SOME SILURIAN BRACHIOPODS FROM GOTLAND

by J. M. HURST

ABSTRACT. In a large collection of brachiopods from the Ludlow of Gotland, epizoan attachment is related to surface shell ornament and rib angularity. '*Camarotoechia*' *nucula* has lateral inhalant canals which are indicated by *Cornulites* encrusting that part of the host shell. The distribution of *Spirorbis* suggests that '*Camarotoechia*' *nucula* and *Homoeospira baylei* lived with the pedicle valve up, whilst *Ptychopleurella bouchardi* lived with the anterior commissure up.

OVER 500 brachiopods were collected from one horizon in the lower Eke Beds (middle Ludlow) of Laubackar, Eastern Gotland, Sweden, about 1·25 kilometres east-north-east of the church of Lau. The Eke Beds are represented by 15 metres of argillaceous limestones alternating with arenaceous marlstone (Hede 1960). The collection studied from Laubackar came from an arenaceous marlstone.

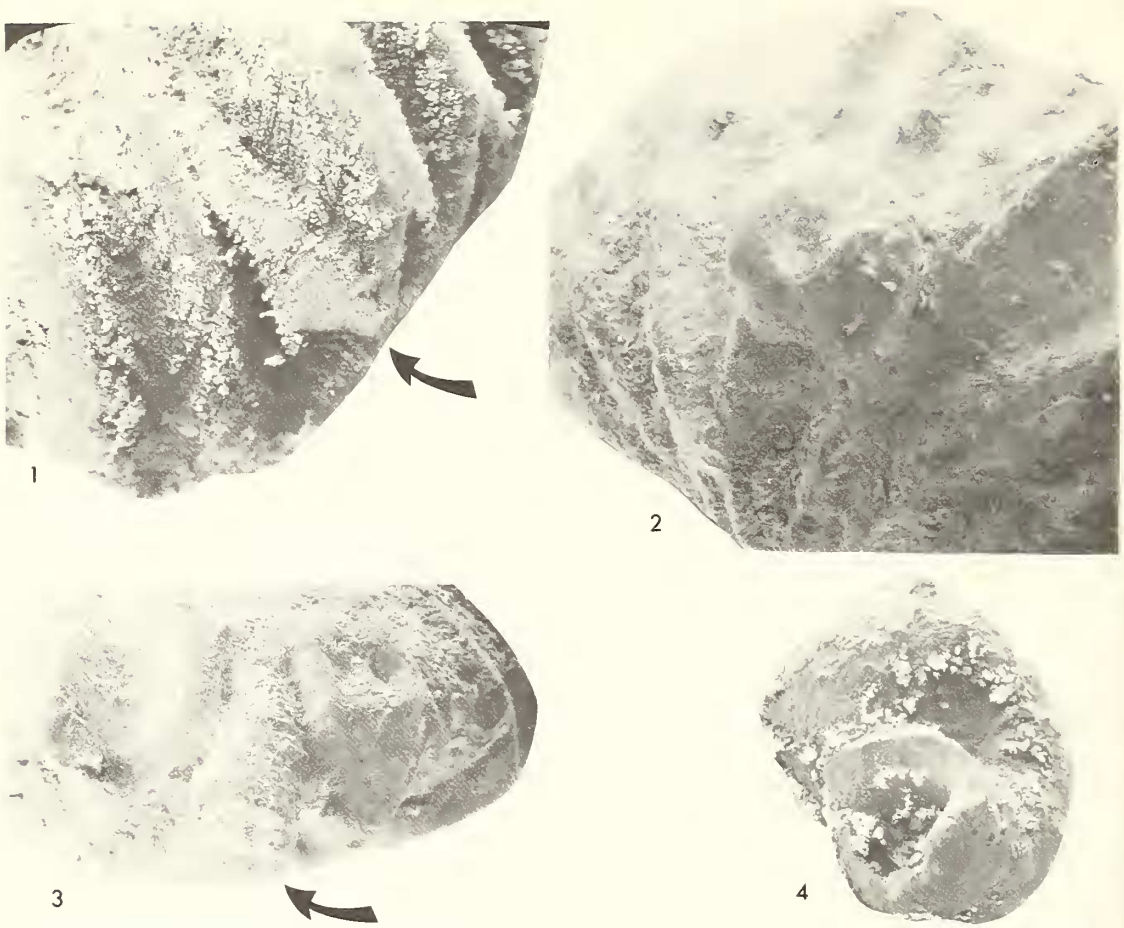
TABLE 1. Composition of encrusting fauna on the different Brachiopods.

Brachiopod species	Number of brachiopod individuals	Brachiopods encrusted by *Spirorbis* %	Brachiopods encrusted by *Cornulites* %	Brachiopods encrusted by *Berenicea* %	Brachiopods with no epizoans %
Ptychopleurella bouchardi	41	96	3	8	4
'*Camarotoechia*' *nucula*	91	15	22	11	62
Homoeospira baylei	120	30	21	2	57
Delthyris elevata	93	2	3	3	93
Spinatrypa sp.	57	15	6	10	73
Glassia obovata	37	8	8	0	84

The most abundant species are (with percentage occurrence following): *Ptychopleurella bouchardi* (Davidson) 9·1%; '*Camarotoechia*' *nucula* (J. de C. Sowerby) 28·3 %; *Homoeospira baylei* (Davidson) 40·8%; *Glassia obovata* (J. de C. Sowerby) 4·2%; *Delthyris elevata* (Dalman) 9·8%; and *Spinatrypa sp.* 6·6%. These six species have an encrusting fauna consisting of: (1) a serpulid worm *Spirorbis* aff. *lewisii* (J. de C. Sowerby); (2) a bryozoan *Berenicea* aff. *consimilis* (Lamx); and (3) *Cornulites serpuliformis* (Vine). Until recently the systematic position of the cornulitids was unknown. Originally they were thought to be tubicular annelids (Nicholson 1872). Fisher (1962) drew attention to the resemblance of some cornulitids to the coelenterates, or some fusulines. However, on the basis of the similarity of some aspects of the shell structure of both cornulitids and molluscs Blind (1972) indicates that they should be placed with the primitive Mollusca.

A commensal relationship between the host brachiopod and the encrusting fauna is suggested by the following observations. (1) Very few cases have been found of *Berenicea*, *Spirorbis*, or *Cornulites* crossing the hinge line or the anterior commissue

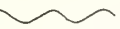
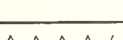
[Palaeontology, Vol. 17, Part 2, 1974, pp. 423–429.]



TEXT-FIG. 1. 1, '*Camarotoechia*' *nucula* with *Cornulites serpuliformis* (arrowed), ×24. 2, *Ptychopleurella bouchardi*, encrusted by *Spirorbis* aff. *lewisii*, ×20. 3, *Homoeospira baylei* with *Cornulites serpuliformis* (arrowed) overhanging anterior commissure, ×24. 4, *Spirorbis lewisii*, ×24.

of the brachiopods. Presumably if they did they would have had a detrimental effect, as the host animal would probably have been unable to open its valves. (2) The only disarticulated specimens in the collection were valves of *Ptychopleurella*, *Spinatrypa*, and *Delthyris*, which represented 12% of the fauna. In one case only was there any encrusting organism on the interior of the valves. This was a small cornulitid which no doubt grew here after the death of the brachiopod. It is concluded that the great majority of the encrusting fauna grew on living brachiopods. If this were not so, both the interior and exterior of diarticulated specimens would have been equally encrusted. (3) In the case of *Cornulites*, specimens at the valve edge can be seen to overhang the shell margin. This is interpreted as the site where water flowed into the mantle cavity. A similar case was reported by Trueman (1942) for *Spirorbis* on non-marine bivalves in the Carboniferous.

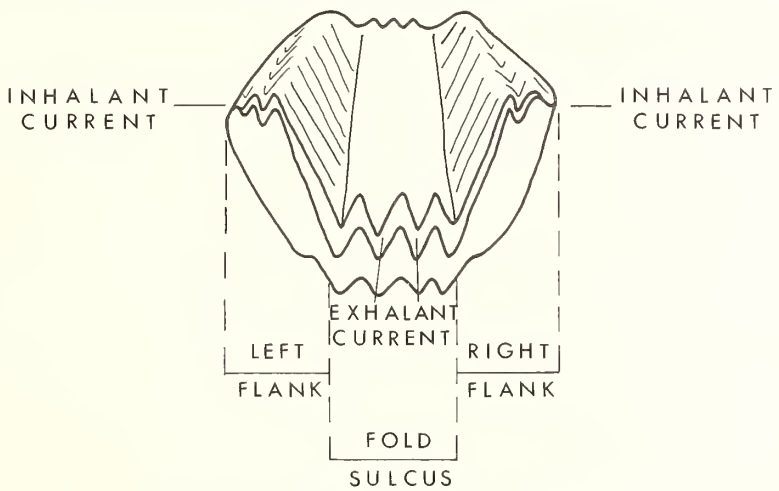
The encrusting fauna (Table 1) is largely restricted to three brachiopod species:

BRACHIOPOD	RIB TYPE
Ptychopleurella bouchardi	
Homoeospira baylei	
'Camarotoechia' nucula	
Delthyris elevata	
Glassia obovata	smooth
Spinatrypa sp.	minute ribs

TEXT-FIG. 2. Brachiopod rib-types.

(1) *Ptychopleurella* is heavily encrusted by *Spirorbis* and little else. (2) '*Camarotoechia*' and *Homoeospira* are encrusted by roughly equal amounts of *Cornulites* and *Spirorbis*, plus a scattering of the bryozoan *Berenicea* (text-fig. 1). The remaining brachiopods *Delthyris*, *Spinatrypa*, and *Glassia* have a low percentage of epizoans.

Spirorbis. *Spirorbis* is the most widespread encrusting faunal element. It is abundant on *Ptychopleurella* and fairly common on '*Camarotoechia*' and *Homoeospira* (Table 2). The explanation for this distribution may lie in the way which *Spirorbis* initially attaches itself to, and grows on, the host shell. Small spirorbids are always situated between ribs, though with growth large spirorbids may cover the ribs. *Ptychopleurella* has low ribs separated by wide shallow grooves, a situation affording the maximum possible protection for serpulid growth. The ribs in *Homoeospira* are stronger and in '*Camarotoechia*' they are extremely angular (text-fig. 2), *Ptychopleurella* has more



TEXT-FIG. 3. Division of '*Camarotoechia*' *nucula*.

spirorbids attached to it than *Homoeospira*, which in turn has more than '*Camarotoechia*' (Table 2). Also the spirorbids attached to *Ptychopleurella* are on the whole far larger than those attached to other species; the spirorbids attached to coarsely ribbed forms may have been prevented from reaching maturity. It would appear that *Spirorbis* prefers to grow in between the host's ribs because of the protection afforded therein, but can develop fully only if the ribs are not angular. *Glassia* is a completely smooth brachiopod, and *Spinatrypa* has little or no rib development. Thus these shells afford less preferential sites for spirorbid encrustation, as does *Delthyris*, which has angular depressions surrounded by low rounded ribs.

TABLE 2. Distribution of *Spirorbis* on Brachiopods.

Brachiopod species	Number of *Spirorbis* on pedicle valve	Number of *Spirorbis* on brachial valve	Total *Spirorbis*
Ptychopleurella bouchardi	112	119	231
'*Camarotoechia*' *nucula*	24	8	32
Homoeospira baylei	31	16	47
Delthyris elevata	4	0	4
Spinatrypa sp.	6	8	14
Glassia obovata	2	1	3

Richards (1972) asserted that the distribution of epizoans on late Ordovician brachiopods was controlled by the size of the brachiopod and its ornament. He also concluded that steeper ribs are a better deterrent to epizoans, than gentle ones. The present study shows that these generalizations also apply at this Gotland locality. Richards also noted that *Platystrophia* produced a mat-like external shell layer of fine spines, which he thought probably acted as another deterrent to epizoans. But *Ptychopleurella*, a member of the closely related subfamily Glyptorthinae, has strong concentric imbrication disposed as frills or drawn out as spines, which clearly did not act as a deterrent to *Spirorbis*. Consequently, *Spirorbis* distribution was probably mainly controlled by the size and angularity of the brachiopod ribs.

Cornulites. *Cornulites* is by no means as widespread or abundant an encrusting faunal element as *Spirorbis* (Table 3). In '*Camarotoechia*' and *Homoeospira*, the majority of the cornulitids are arranged in the grooves, parallel to the ribs of the host shell. The steep ribs of '*Camarotoechia*' and *Homoeospira* carry, in general, larger *Cornulites* than do the smooth or broad-ribbed brachiopods. *Ptychopleurella*, *Delthyris*, and *Spinatrypa* are not sharply ribbed forms, but they are characterized by strong growth lines which are often spinose. The spinose shell morphology is probably a major factor in inhibiting *Cornulites* from encrusting the shell (Richards 1972). The low density of encrusting *Cornulites* on *Glassia* is probably due to the fact the smooth shell offered no protection. Consequently, the distribution of *Cornulites* appears to be limited to sharply ribbed forms, which do not have spinose growth lines. Spinose forms are not a suitable site for *Cornulites* encrustation. *Cornulites* encrustation is accompanied by some absorption of calcium carbonate from the host (Fisher 1962); consequently, the most advantageous place for a cornulitid to grow was in between the ribs of coarsely ribbed shells, as, not only is this

TABLE 3. Distribution of *Cornulites* on Brachiopods.

Brachiopod species	Number of *Cornulites* on pedicle valve	Number of *Cornulites* on brachial valve	Total *Cornulites*
Ptychopleurella bouchardi	0	0	0
'*Camarotoechia*' *nucula*	23	22	45
Homoeospira baylei	27	13	40
Delthyris elevata	2	0	2
Spinatrypa sp.	2	3	5
Glassia obovata	2	1	3

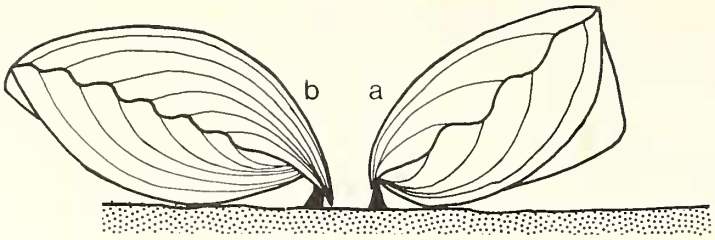
position well protected, but it will allow greater absorption of calcium carbonate from the host brachiopod.

Berenicea. This byrozoan occurs in such low numbers that it provides no conclusions (Table 1).

DISTRIBUTION AND ORIENTATION OF THE ENCRUSTING FAUNA

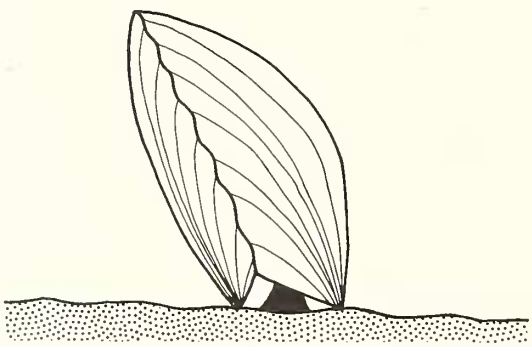
The distribution and orientation of the epizoans may be used to throw light on the possible life positions and feeding habits of the various brachiopods.

'*Camarotoechia*' may be divided into three roughly equal areas, a central fold and sulcus, bounded by two flanks (text-fig. 3). The number of *Cornulites* on these areas was counted on both pedicle and brachial valves. Seventeen and twenty-one specimens of *Cornulites* occurred on the right and left flanks of the brachiopod respectively, whilst only seven occurred in the fold and sulcus region. This distribution is not random as a 97% significance was obtained from a modified Chi-square test (Reyment 1971). This is probably related to the filter feeding system of the brachiopod, with the majority of the cornulitids situated above the lateral inhalant canals (text-fig. 3). In recent rhynchonellid brachiopods, the region of the fold is the site of the exhalant canals (Thomson 1927; Rudwick 1960). Thus the preferential distribution of *Cornulites* on the lateral flanks of Silurian '*Camarotoechia*' conforms with the water movement seen in modern rhynchonellids. The orientation of the cornulitids, on the lateral flanks of '*Camarotoechia*', is in accord with the findings of Schumann (1967). He observed commensal *Cornulites* preferentially attached to the lateral flanks of *Mucrospirifer reidfordi*, from which he concluded that the cornulitids benefited by feeding on the hosts inhalant currents. Hoare and Steller (1967) described a series of epifaunal elements on brachiopods in the Devonian Silica Formation of north-western Ohio. Examination of 3,105 specimens of different genera revealed that the epifaunal elements were distributed unequally in the same way as the Gotland collection. They also give a detailed description of epifaunal host relationships in a specimen of the Devonian brachiopod *Paraspirifer brownockeri* associated with a boring sponge, *Cornulites*, an articulate brachiopod and bryozoa. They note that *Cornulites* is orientated in an anterior direction, their direction of growth controlled by the grooves in the shell, and conclude that this relationship appears to be commensal with *Cornulites* benefiting from the current action of the host. The distribution of *Cornulites* on *Homoeospira* was tested, but was found to be a totally random one.



TEXT-FIG. 4. Life position of '*Camarotoechia*' *nucula* (*a*) and *Homoeospira baylei* (*b*).

Spirorbis has a totally different commensal association with the brachiopods, as it is not related to the inhalant or exhalant canal system. On '*Camarotoechia*' and *Homoeospira*, *Spirorbis* prefers the pedicle valve. If *Spirorbis* preferred clearer water, to the ejected waste, it would attach itself to the parts of the brachiopod furthest away from the substrate, so that its feeding system is not polluted by mud. Consequently, *Spirorbis* encrustation on *Homoeospira* and '*Camarotoechia*' may indicate the life position of these brachiopods. The heavily encrusted pedicle valve was probably uppermost (text-fig. 4). By contrast the even distribution of *Spirorbis* on both pedicle and brachial valves of *Ptychopleurella* suggests that this brachiopod lived with both valves inclined at a high angle to the substrate (text-fig. 5). Ager (1961) found that *Spirorbis* had a general distribution on the Devonian spirifer *Spinocyrtia iowensis*. From this he concluded, as is the case here, that *Spirorbis* had no relation to the feeding habits of the host.



TEXT-FIG. 5. Life position of *Ptychopleurella bouchardi*.

CONCLUSIONS

1. *Cornulites* preferred to grow in the grooves of strongly ribbed brachiopods.
2. *Spirorbis* shows a preference for broad-ribbed brachiopods like *Ptychopleurella*.
3. '*Camarotoechia*' has lateral inhalant canals which are indicated by *Cornulites* encrusting that part of the host shell.
4. The distribution of *Spirorbis* suggests that '*Camarotoechia*' and *Homoeospira* lived with the pedicle valve up, whilst *Ptychopleurella* lived with the anterior commissure up.

This concentration of encrusting fauna is of local occurrence. Other collections from the Eke Beds and other horizons in the Ludlow of Gotland, have a very low density of epizoans, when compared to this one. The high density of brachiopods, at this one locality, suggests that deposition was slow. In this environment, the brachiopods appear to have provided the only suitable substrate for encrustation by epizoans.

Acknowledgements. I wish to express my sincere thanks to Mr. C. Richardson for help in collecting the fossils. I am also grateful to Dr. L. R. M. Cocks, Dr. W. S. McKerrow, Mr. F. Fürsich, Mr. R. Watkins, and Mr. R. Sykes for reading the manuscript and suggesting improvements. The work was supported by a Natural Environment Research Council Grant.

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Revised typescript received 10 October 1973